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A New Approach to Evaluating Troop Deployment in Wild Japanese Monkeys

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In winter when the mountain slopes are covered with deep snow, it is easy to obtain quantitative data on the two-dimensional deployment of members of a troop of wild Japanese monkeys. We observed the deployment of a troop on a slope from the opposite side of a river. The deployment patterns, evaluated on the basis of the relative distance from the central point (centroid) of the troop, were different for each sex and age category. Adult females, infants, and 1-year-olds tended to be grouped together and were concentrated near the center of the troop. On the other hand, adult males were randomly spaced. These tendencies suggest that the deployment reflects the social structure of the duplicate concentric-circle model originally proposed by J. Itani (1954).

KEY WORDS: Japanese monkeys; troop deployment; computer analysis; duplicate concentric-circle model.

INTRODUCTION

Since 1948, the ecology and sociology of Japanese monkeys (*Macaca fuscata fuscata*) have been investigated in provisioned areas or in the wild. Itani (1954) first proposed the duplicate concentric-circle model for the social structure of Japanese monkeys. There were, however, no field studies which had examined the deployment of an entire troop in the wild.

Kawamura (1956) first described deployment at a provisioned feeding ground of the Koshima troop in terms of the status and behavior of the monkeys. Mano (1972) pointed out that the dominance rank system was

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reflected in the deployment of the central and peripheral parts of the provisioned Arashiyama A and B troops. Mori (1977) examined the spacing of limited numbers of individuals of the Koshima troop at a provisioned feeding ground and in the forest. Chivers (1971) investigated the average interindividual distances of a siamang group during different activities, at different seasons of the year, and with changing social relations within the group. Observing unidimensional troop deployment (progression) in yellow baboons, Rhine (1975), Rhine and Westlund (1981), and Altmann (1979) indicated the sociological function of individual ordinal positions. Kawai and Mori (1979) studied the deployment of the entire membership of single and plural units of gelada baboons, but they did not evaluate the entire membership of the herd in this way.

These studies dealt with the deployment of a troop in limited ecological conditions or analyzed only unidimensional progression. Since it is quite difficult to observe an entire troop at a time, there have been a few investigations of the two-dimensional deployment of ecological units as a whole in primates.

The present study represents the first attempt to obtain quantitative data on the two-dimensional deployment of all the members of a troop of Japanese monkeys in the wild. We focused on establishing a suitable methodology for recording and analyzing data on deployment.

METHODS

Subject Troop

We studied the Shiga A_2 troop in Shiga Heights, Nagano Prefecture, central Japan. The Shiga A troop, which had been provisioned at Jigokudani since 1963, split into two troops in 1979. One troop was named the Shiga A_1 troop. It continued to be provisioned at Jigokudani. The other troop was named the Shiga A_2 troop. It shifted from the provisioned area to the forest. The winter home range of the A_2 troop is located on the steep mountainsides along the middle part of the Yokoyugawa Valley (Fig. 1). Further socioecological information on the A_2 and adjacent troops has been given by Wada and Ichiki (1980), Tokida (1981), Wada and Tokida (1981), and Wada (1983). Table I shows the sex and age composition of the A_2 troop in February 1980.

Collection of Deployment Data

For 20 days during February and March 1980, the two-dimensional deployment of members of the Shiga A_2 troop was observed from across

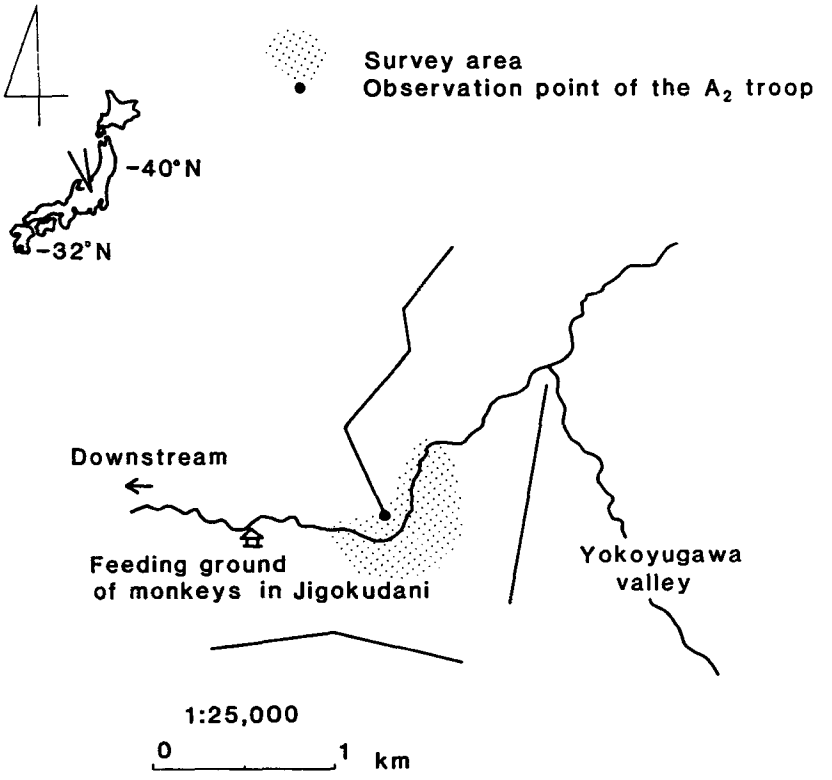

Fig. 1. Map of the survey area.

Table I. Sex and Age Composition of the Shiga A_2 Troop in February 1980

Category of individuals	Number of individuals
Infant	10
1-year-old	9
2-year-old	7
3-year-old	6
4-year-old male	2
5-year-old male	1
6-year-old male	2
Adult female	19
Adult male	4
Total	60

the valley. The area is covered by secondary deciduous broad-leaved forest, where *Fagus crenata* dominated until disturbed by small-scale forest-cutting about 10 years ago. The trees become completely defoliated in winter, from December to March, affording an unobstructed view. The mountainsides are very steep and are covered with snow to a depth of about 2 m, which slows down troop progression. Winter thus provides good conditions for monitoring the positions of individual animals and transforming them into two-dimensional records.

The observer used a recording sheet (section paper, 24 × 18 cm), on which prominent stones and trees had been marked in advance. The actual distances between these prominent markers were measured afterward. The observer, on the opposite side of the valley, utilized binoculars and monoculars to detect the individuals of the troop and marked their positions on the recording sheet. The place of observation was situated approximately 200 m away from the troop across the valley. Once every 30 min the positions of the individuals were scanned and recorded. This scanning required about 7 min. In periodic scans, an assistant observer with a transceiver approached the troop to obtain further information about the sex and age of the individuals. As a result, a total of 109 scans was completed in 20 days, yielding a cumulative total of 3471 individual deployments (Table II). The

Table II. Observation Records of the Shiga A_2 Troop

Date	Number of scans	Total number of individuals in daily scanning[a]
Feb.		
19	3	81
20	8	249
21	5	126
22	11	379
23	4	112
24	5	107
25	10	417
26	5	153
27	6	235
28	8	203
29	9	221
Mar.		
1	0	0
2	10	427
3	3	65
4	0	0
5	6	189
6	6	128
7	7	290
8	0	0
9	3	89
Total	109	3471

[a]The mean number of individuals recognized at one scanning was 32.

number of individuals recognized at one scanning was 32 ± 12 (mean ± SD). The disappearance rate of individuals from scan to scan was random with respect to sex and age. Adult males included individuals of seven years and older. Adult females included individuals of 4 years and older. The scanning samples included data taken while the troop was progressing, feeding, resting, etc.

Storage of Deployment Data

The positional and sex-age information on the 3471 individuals, recorded on the 109 sheets, was processed and stored in a minicomputer (PDP 11/34, DEC). The positional information on the recording sheets was read by an X-Y axis digitizer (DSCAN, Seiko). Individuals were classified into 13 categories, representing different sex and age classes, as indicated in the first column in Table III. Standard MUMPS was used as the programming language.

Analysis of Deployment Data

We devised two kinds of measurements for evaluating the deployment of individuals within the troop. One was measurement of the relative distance from the central point (centroid) of the troop, and the other was measurement of the relative distance from a specific individual. The two approaches thus differed with regard to the origin (that is, the focal point) from which the distance was evaluated. Although these two kinds of measurements were not totally independent, they did provide differing means of describing the deployment of the troop. In the first measurement, utilizing the central point of the troop as the origin, each set of deployment data (109 examples) was arranged relative to the point having the mean values on both the X and the Y axes. This point was thus the centroid of the troop. At first, the distance of each individual from the central point was calculated. Then, the longest individual distance, i.e., the distance from the central point to the most distant individual, was divided into 10 equal intervals. The longest distance was different at each scanning, and it was used as the radius of a circle within which all members of the troop could be contained. The distribution of individuals around the central point was evaluated on the basis of relative grades of distance (Fig. 2). Such measurements expressed the central and peripheral locational tendencies of each sex-age category of monkeys.

In the second measurement, utilizing a specific individual as the origin, individuals belonging to the category of "infant" were taken as the focal point. The procedure for evaluating the distance from the infant was identical to the first measurement described above. A cumulative total of 482 infants, found in the 109 examples, served as focal points. The distances from one

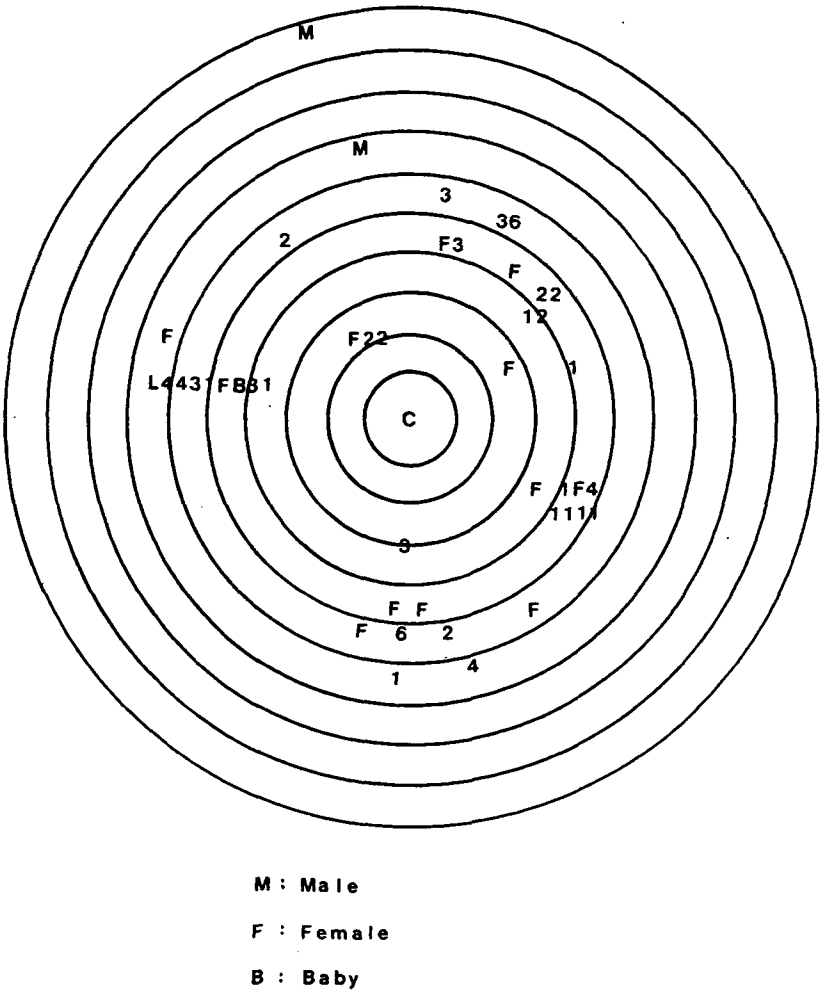

Fig. 2. Example of deployment of the troop from which the relative grades of distance were calculated (central-point method). Each letter or numeral represents one monkey in each category.

specific infant to each other individual were calculated. The distance from the specified infant to itself (zero distance) was not included. The longest distance from the infant, divided into 10 equal intervals, provided the basis for comparing the relative distances. Such measurements demonstrated how each category of monkeys was distributed around the infant. Although similar analyses were performed for the other categories, only the results centered on infants are reported here.

Table III. Dispersal of Monkeys Around the Central Point Taken as the Focal Point in the Shiga A_2 Troop

Category of individuals	Number of individuals in grade[a]										
	1	2	3	4	5	6	7	8	9	10	Total
Adult male	8	30	18	31	27	26	33	40	22	57	292
Adult female	42	78	87	103	98	92	73	39	42	34	688
Infant	31	81	95	82	66	38	32	19	20	18	482
1-year-old	25	48	51	56	55	41	35	16	16	16	359
2-year-old	26	38	46	54	58	39	31	27	20	22	361
3-year-old	10	21	22	42	30	33	19	17	14	16	224
4-year-old male	4	15	10	12	17	12	12	8	4	16	110
5-year-old male	4	6	11	7	5	6	4	6	4	11	64
6-year-old male	1	1	3	5	3	6	5	4	2	8	38
Unknown (large size)	4	2	5	7	6	12	6	4	4	11	61
Unknown (middle size)	0	0	0	1	1	1	0	2	4	2	11
Unknown (small size)	0	2	2	0	0	1	1	0	0	0	5
Unknown	55	71	94	95	112	109	84	65	45	46	776
Total	210	393	444	495	478	416	334	247	197	257	3471

[a]The grade represents the relative distance from the central point in each scanning.

RESULTS

Deployment Evaluated by the Relative Distance from the Central Point of the Troop

The distribution of the cumulative total number of individuals observed (Table III) was plotted between the first and the tenth grades, and the expected curve for a random distribution was also drawn (Fig. 3). Clearly, if the monkeys were distributed at random within a circular area, the expected ratios of numbers of monkeys in any two regions would be in proportion to their areas. In the present analysis, the area occupied by the troop was divided into 10 concentric circles of radius 1, 2,..., 10 units, respectively. The area within the first circle (radius 1) was thus 1π, that in the annulus between the first and the second circles was 3π, etc., and the total area was 100π. The expected fraction of the troop within the first circle was $1\pi/100\pi$ (1%), that between the first and the second circles was $3\pi/100\pi$ (3%), etc., up to the outermost annulus, which would, on average, include 19% of the monkeys. If the area occupied by the group was more elongated than a circle, as it sometimes was, then a smaller difference in the areas of the inner and outer annuli, as well as in the corresponding numbers of monkeys in each, would be expected.

As shown in Fig. 3, the observed numbers of individuals exceeded the values expected from a random distribution at grades 1-6 but were lower

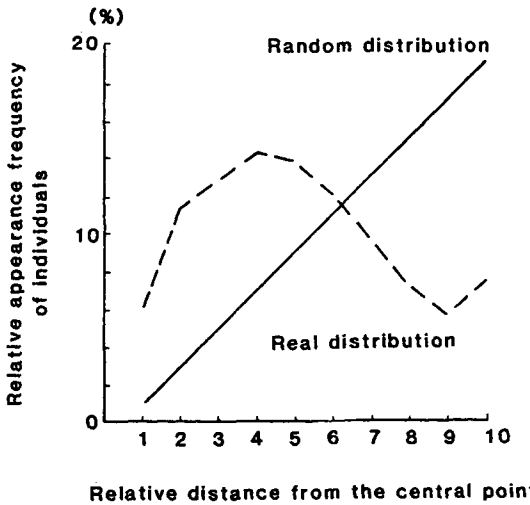

Fig. 3. Real and random distribution of total individuals for the total scanning data.

at grades 7-10. This means that the individuals tended to be concentrated in the "central" area (grades 1-6) and dispersed in the "peripheral" area (grades 7-10). Since the most distant individual was used to determine the limit of grade 10, this grade, unlike all others, could not have a total value of zero. In grade 10, the total numbers for all sex-age classes combined were necessari-

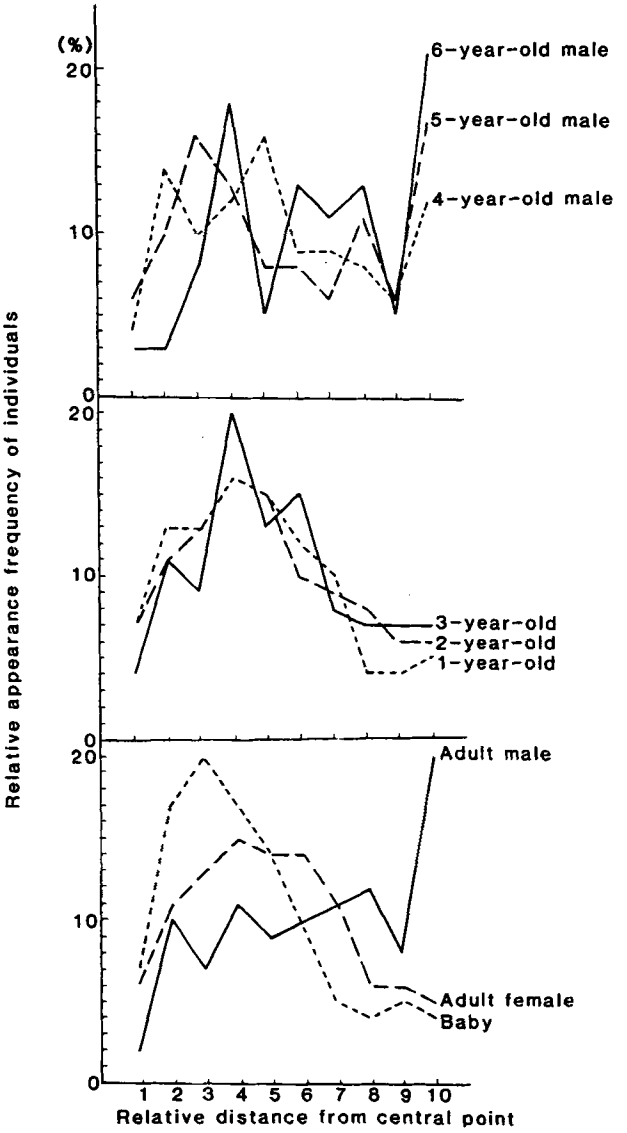

Fig. 4. Deployment characteristics of each category of individuals around the central point.

ly at least as large as the number of scanning samples, since in each sample there was at least one individual in the 10th grade. This one individual, of the average of 32 individuals in the troop, represented a value of about 3%, so that the figures for the 10th grade were, to some extent, artificially high. There was no obvious way to avoid this defect, but it appeared to have negligible effects.

It was shown that the deployment pattern differed among each sex and age category based on the relative distance from the central point (Fig. 4). In the case of infants, the numbers of observed individuals reached a maximum in grade 3 and were relatively high in grades 2, 4, and 5 but decreased remarkably thereafter. It should be borne in mind, however, that the areas in each grade increased progressively outward. The distribution of adult females showed similar tendencies in its deployment pattern to those of infants.

The distribution pattern of adult males resembled, to some extent, the expected random distribution. In contrast to the adult female/infant type of distribution, the numbers of males increased broadly with grade in proportion to area. This suggests that adult males may be randomly distributed in the deployment of a troop.

In the case of 1-, 2-, and 3-year-olds of both sexes, the distribution patterns were intermediate between that of the adult female/infant and that of

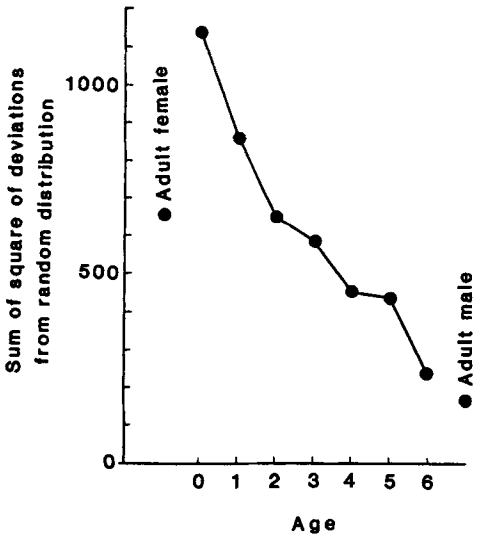

Fig. 5. Deviation from the expected random distribution in each sex-age category. Ages of 3 years include both sexes; those of 4 to 6 years include males only.

the adult male types. The patterns of the 4-, 5-, and 6-year-old males approached more closely that of adult males than that of younger animals.

To evaluate the degree of similarity to the expected random distribution, we carried out quantitative goodness-of-fit tests for the distribution of the sex-age categories (Fig. 5). For this purpose, the values in Table III were transformed into percentages. The square of the deviation from the expected random distribution in each of the 10 intervals was calculated, and their sum was obtained as a deviation index. The deviation from the expected random distribution decreased progressively with age from 0 to 6 years and approached the level of the adult male, which was most similar to the random distribution.

Based on the above-mentioned tendencies, the deployment patterns were divided into three types: (1) the adult female/infant type, (2) the adult male type, and (3) the intermediate type.

Summarizing the data obtained, it can be said, in general, that infants and adult females tend to occupy the central part of the troop, while the spatial distribution of the adult males is random. In terms of the relative frequencies of each sex and age category in each grade, adult males show a stronger tendency to occupy peripheral grades. The adult males reveal no tendency to stay near infants or adult females, and their greater relative frequency in the peripheral areas (Fig. 6) must reflect the centripetal tendencies of the other members of the troop.

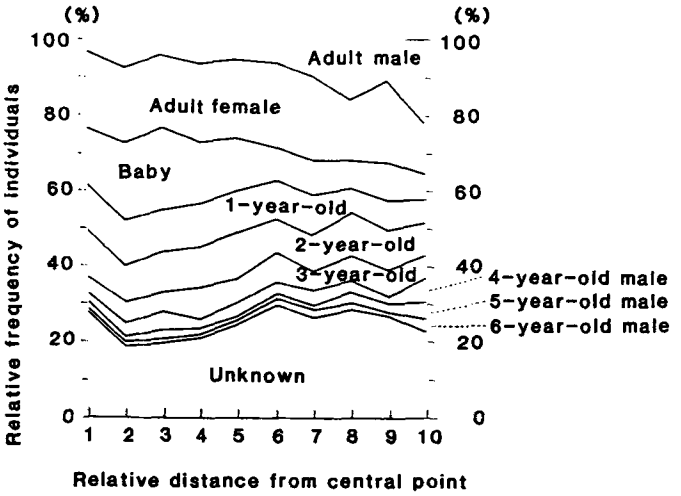

Fig. 6. Sex and age composition ratio in each grade of relative distance.

Table IV. Dispersal of Monkeys Around Each Infant Taken as the Focal Point in the Shiga A_3 Troop

Category of individuals	Number of individuals in grade[a]										
	1	2	3	4	5	6	7	8	9	10	Total
Adult male	95	162	142	146	114	105	136	113	104	288	1,407
Adult female	536	522	460	407	310	274	297	284	253	249	3,601
Infant	634	394	272	212	189	195	163	154	112	117	2,442
1-year-old	338	313	264	212	145	164	127	159	130	128	1,980
2-year-old	207	247	235	205	191	183	165	138	165	131	1,867
3-year-old	91	154	167	152	114	83	78	78	67	139	1,123
4-year-old male	64	65	77	57	63	56	44	48	50	53	577
5-year-old male	38	34	32	38	32	20	21	18	36	49	318
6-year-old male	10	33	21	22	18	18	15	25	26	43	231
Unknown (large size)	12	50	37	27	24	25	21	34	23	46	299
Unknown (middle size)	0	1	1	4	4	6	5	8	11	2	42
Unknown (small size)	2	5	10	5	3	7	2	0	0	0	34
Unknown	227	310	349	205	300	266	257	217	216	224	2,651
Total	2,254	2,290	2,076	1,772	1,507	1,402	1,333	1,276	1,193	1,469	16,572

[a]The grade represents the relative distance from each selected infant.

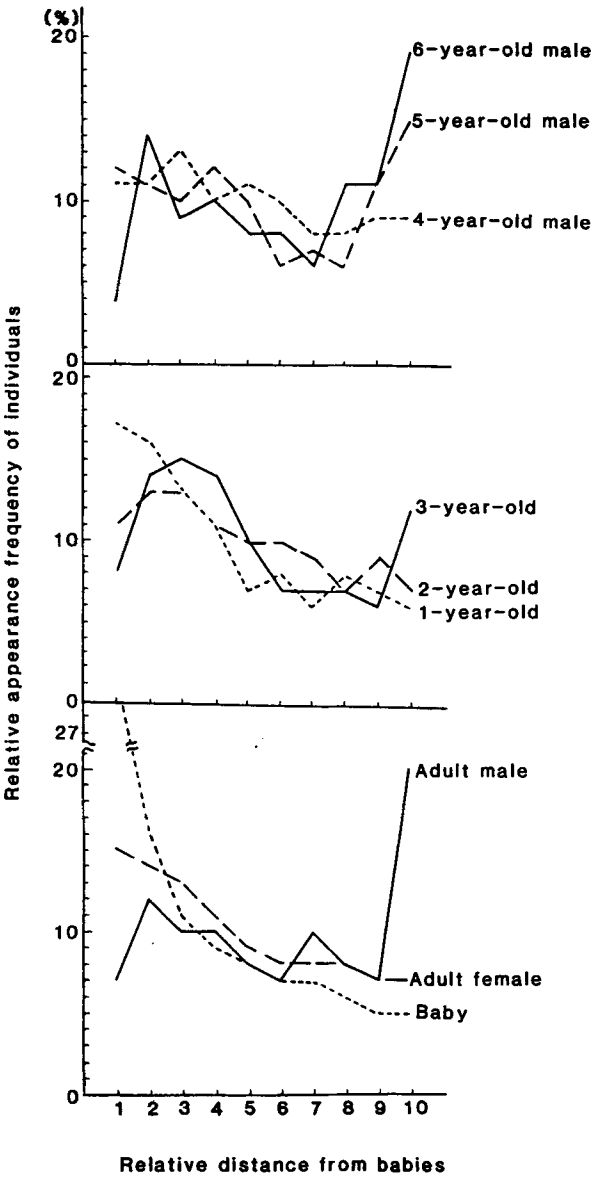

Fig. 7. Deployment characteristics of each category of individuals around infants.

Deployment Evaluated with the Relative Distance from Each Infant as the Focal Point

The observed total number of individuals around infants was higher in grades 1 and 2 and decreased progressively in the other grades (Table IV). This pattern differed from that of individuals around the central point, in which the highest number was in grade 4. The high infant-to-infant values at grades 1 and 2 in Fig. 6 mean that infants were often situated together.

At grade 1, infants accounted for the highest number, followed by 1-year-olds and adult females. If mothers could be distinguished from other adult females, they would probably obtain values similar to those of infants in grade 1. Infants decreased markedly in grades 2 to 3 and gradually to grade 4 and beyond. The decreasing tendency of numbers of individuals after grade 1 was similar for 1-year-olds and adult females (Fig. 7). On the other hand, adult males were lower at grade 1 and increased rapidly at grade 10. The distribution patterns of 2- to 6-year-old males revealed types intermediate between that of infants and that of adult males (Fig. 7). The data also indicated that, with advancing age, both sexes of 2- and 3-year-olds and males 4 years old and over tended to migrate to the peripheral area.

Thus, the two methods of measuring relative distance, one from the central point and the other from specific infants, yielded similar results. The data suggest that, in general, infants, 1-year-olds, and adult females tend to group together, while adult males are randomly distributed.

DISCUSSION

Ecological studies of Japanese monkeys originally began at Mt. Takasakiyama (Itani, 1954). Since the 1960s, the ecology of Japanese monkeys living in snowy and snow-free areas has been investigated by many researchers. Few studies have dealt with the spatial distribution of the whole troop due to the difficulty of observing the entire troop at the same time. This difficulty was overcome in the present study by using snow-covered slopes which allowed good observation in winter. This unique setting on the snowy mountainsides in Shiga Heights afforded a two-dimensional view of the entire troop.

On the basis of 109 sets of scanning data, the deployment patterns were divided into three types: (1) the female/infant type, (2) the adult male type, and (3) the intermediate type. The troop deployment underwent changes according to both the phase of troop movement and complicated environmental factors. Despite the confounding influence of such variables, however, some characteristics of the deployment patterns can be shown to reflect the

ecological and sociological relationships in the troop. As illustrated in the figures, infants, adult females, and 1-year-olds showed similar patterns of distribution and were usually situated in the central part of the troop. This may indicate simply that the mother tends to be with her offspring as observed in provisioned troops. A high infant-to-infant proximity was also noted (Fig. 7), suggesting that infants tend to gather together. The birth season of the Japanese monkeys in Shiga Heights is mainly during April and June, so that the infants were sufficiently independent by winter to begin integrating socially into the troop.

The adult males were randomly spaced, without any obviously strong link with other categories of individuals in the troop deployment.

Itani (1954) recognized "central" and "peripheral" parts in the social structure of the provisioned troop. He represented the social structure as a duplicate concentric-circle model. Mano (1972) defined the central part of a troop as the area surrounded by a line connecting the outermost adult females and juveniles and the peripheral part as the area outside the central part. The central part of such a troop is composed mainly of groups of adult females, infants, and 1-year-olds. The centripetal tendency noted in our observations appeared to correspond to this central part of the troop, which had not previously been defined quantitatively. It should also be pointed out that males gradually separated from the mother offspring groups as they matured, while females tended to remain. The males' separation from the mother/offspring group is clearly illustrated in Fig. 4, where 4-year-olds and over show a progressive increase at grade 10.

The above findings confirm the existence of a central part of the troop composed of females, infants, and young offspring, and a peripheral part which can be recognized consistently outside the central part through various conditions of the troop. The central part of the troop can be defined approximately as the part within grade 6 (Fig. 3). Although the structure and function of troops have been studied mainly on the basis of observations of provisioned troops, this study has demonstrated that a similar structure is recognizable even in forest-living troops.

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